
Revision of the Cretaceous Fossil Genus *Palaeoaster* (Papaveraceae) and Clarification of Pertinent Species of *Eriocaulon*, *Palaeoaster*, and *Sterculiocarpus*

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ABSTRACT. The fossil organ genus *Palaeoaster* (Papaveraceae), from the Cretaceous Western Interior of North America, is revised to contain a single species, the new combination *P. porosa*. The type status is clarified and lectotypes are selected for the basionym *Eriocaulon? porosum* (Eriocaulaceae) and synonyms *P. inquirenda*, *P? similis*, and *Sterculiocarpus coloradensis* (Sterculiaceae). This revision reflects an informal circumscription of *Palaeoaster* in use since the late 1930s, and is the first of several papers on this genus.

Key words: Cretaceous, *Eriocaulon*, fossil, North America, *Palaeoaster*, Papaveraceae, *Sterculiocarpus*.

Since the 1870s, *Palaeoaster* has been a familiar and sometimes controversial element in the fossil record of the latest Cretaceous Western Interior of North America, where this fossil occurs from 74.5 MY (million years) in the Fruitland Formation in New Mexico to 64.5 MY in the Hell Creek Formation in North Dakota (Smith, 2000). Although this fossil was important to historical debates about the stratigraphic position of the Cretaceous–Tertiary boundary in the Western Interior, its morphological identity and taxonomic affinity remained unknown for over a century; *Palaeoaster* has often been described as “problematic” (e.g., Brown, 1962).

Palaeoaster, originally *incertae sedis*, is a large capsular fruit related to the basal eudicot family Papaveraceae (Smith, 2000, in press; Figs. 1, 2). The fruit dehisces, forming long valves. All specimens of *Palaeoaster* described prior to 1932 are dehisced fruits, missing some of their valves, that were misinterpreted as clusters of leaves. Apparently, the name *Palaeoaster* reflects the superficial resemblance between these putative leaves and the involucre of *Aster* and other genera of Asteraceae.

Knowlton (1917) based the genus *Palaeoaster* on his new species, *P. inquirenda*, not on the earlier *Eriocaulon? porosum* (Lesquereux, 1874). However,

as suggested by a number of paleobotanists and as confirmed by my examination of original material, the relevant specimens all belong to a single species. Lesquereux’s name is older, but cannot be retained because it applies to an unrelated extant genus, so a new combination in *Palaeoaster* is required. Per the ICBN (Greuter et al., 2000) Article 7.4, the type of the new combination *P. porosa* is the lectotype of the basionym *Eriocaulon? porosum*; however, per Article 7.2, the type of the genus *Palaeoaster* remains the lectotype of *P. inquirenda*.

Palaeoaster F. H. Knowlton, Fossil Floras of the Vermejo and Raton Formations of Colorado and New Mexico: 278. 1917. TYPE: *Palaeoaster inquirenda* F. H. Knowlton.

1. Palaeoaster porosa (Lesquereux) U. R. Smith, comb. nov. Basionym: *Eriocaulon? porosum* Lesquereux, [7th] Annual Report of the United States Geological and Geographical Survey of the Territories: 396. 1874. TYPE: U.S.A. Colorado: “Sand Creek,” 1873, W. H. Holmes (lectotype, selected here, USNM 137).

Palaeoaster inquirenda F. H. Knowlton, Fossil Floras of the Vermejo and Raton Formations of Colorado and New Mexico: 278. 1917. Syn. nov. TYPE: U.S.A. Colorado: “Alkali Gap,” 1910, W. T. Lee and others (lectotype, selected here, USNM 34527).

Lectoparatypes, selected here, USNM 458511, 458512, 458513, 458514.

Palaeoaster? similis F. H. Knowlton, Laramie fl. Denver: 168. 1922. Syn. nov. TYPE: U.S.A. Colorado: “Murphy coal bank” on Ralston Creek, 1890, A. Lakes (lectotype, selected here, USNM 36804).

Lectoparatype, selected here, USNM 36803.

Sterculiocarpus coloradensis E. W. Berry, J. Wash. Acad. Sci. 22: 119. 1932. Syn. nov. TYPE: U.S.A. Colorado: Ramah, C. Shelton s.n. (holotype, as of 1995 property of V. Shelton).



Figure 1. Specimen 4380, a dehiscent fruit of *Palaeoaster* from the excavation site of the spectacular *Tyrannosaurus rex* specimen BHI 3033 ("STAN"); the inner faces of the valves are preserved as impressions in sandstone. Collected by Neal L. Larson and others. Scale bar = 1 cm.

The original description of *Eriocaulon? porosum* (Lesquereux, 1874: 396) does not show or designate the single specimen on which it is based; figures added to a reprint of that description (Lesquereux, 1878: 106, pl. 16, figs. 2–2a) show *Palaeoaster* specimen USNM 137. Additional specimens of *Palaeoaster* were identified as *E? porosum* by Knowlton (Gale, 1910; Lee, 1912; Knowlton, 1930). *Eriocaulon* is an extant genus of the monocot family Eriocaulaceae. Despite warnings that the taxonomic assignment of *E? porosum* to *Eriocaulon* was based on superficial evidence (Lesquereux, 1878; Knowlton, 1930: 132–133), numerous authors accepted this species as fossil evidence of Eriocaulaceae (Coulter & Chamberlain, 1903; Marty, 1907; Horwood, 1912; Chesters et al., 1967; Nĕmejc, 1975). Daghljan (1981) excluded *E? porosum* from Eriocaulaceae, leaving this species *incertae sedis*.

In his original description of *Palaeoaster inquirenda*, Knowlton (1917: 278, pl. 49, figs. 5, 6) stated that "the type specimens . . . are contained in a large collection from Alkali Gap." The collection from this locality at USNM contains the figured specimen, USNM 34527, and four other specimens of *Palaeoaster*. Knowlton (1917) described *P. inquirenda* ambiguously as "leaves" or a "capsule" (his quotes), based on specimens that he removed from *Eriocaulon? porosum*. However, Knowlton's concept of these two species is badly flawed: he assigned specimens found above the Cretaceous–Tertiary boundary (as recognized then) to *E? porosum*, and specimens found below the boundary to *P. inquirenda*, without noting any clear morphological differences (there are none). Knowlton then used these two species to locate the Cretaceous–

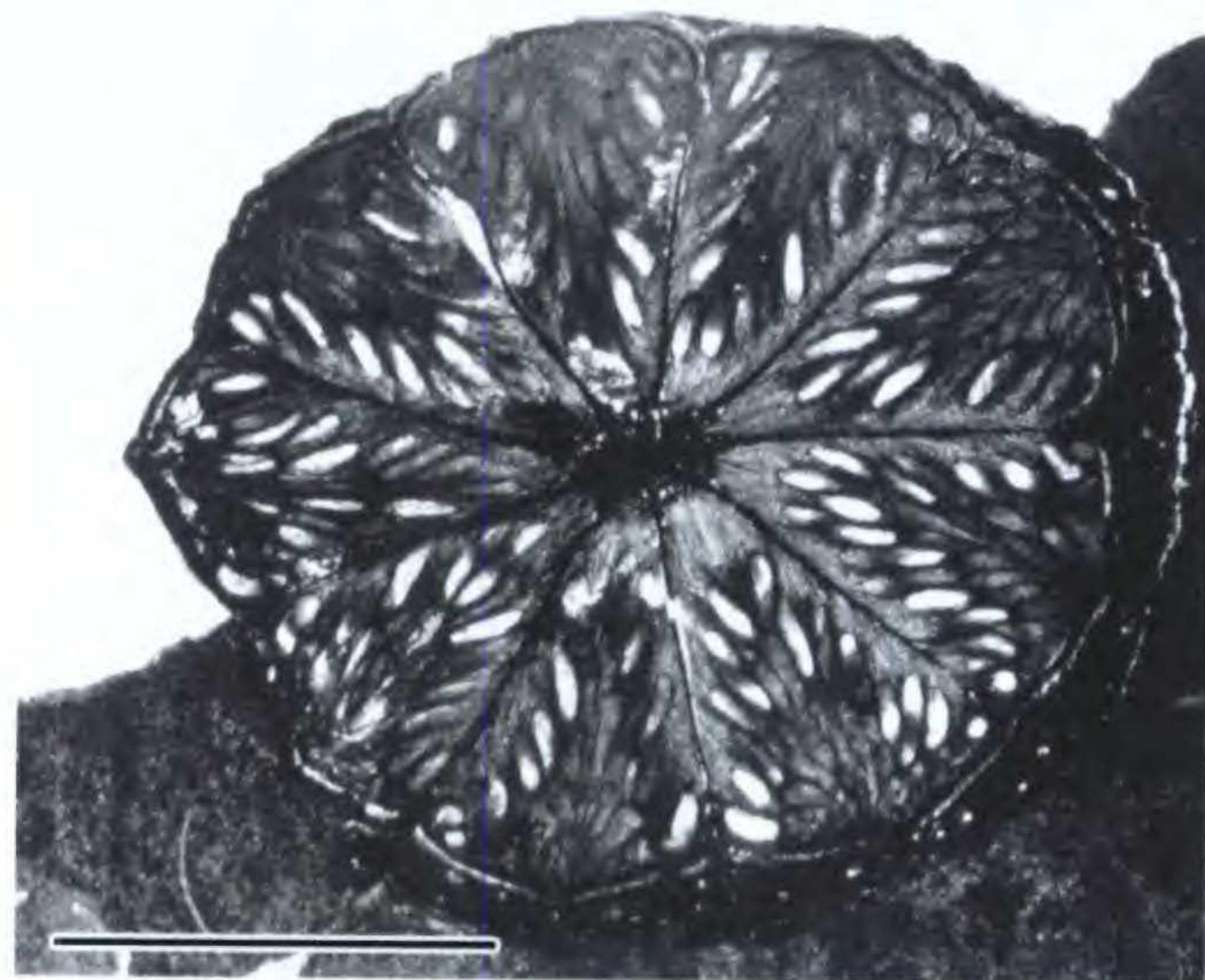


Figure 2. Specimen BHI 4001, cross section of a permineralized fruit of *Palaeoaster*. Collected by the Black Hills Institute. Scale bar = 1 cm.

Tertiary boundary (e.g., Knowlton, 1930), thereby introducing a circularity problem into the stratigraphy of the Western Interior. Brown (1943: 72) considered *P. inquirenda* to be a synonym of *E? porosum*, but did not make the required new combination.

Knowlton (1919: 427) created *Palaeoaster? similis* as a *nomen nudum*. In his later description, Knowlton (1922: 168, pl. 24, figs. 10–11) figured two specimens of *Palaeoaster* but did not select one of them as the holotype; USNM 36804 is the more complete specimen. Knowlton (1922) remarked that individual "leaves" (his quotes) of *P? similis* are "practically indistinguishable" from those of *P. inquirenda*; it appears that he distinguished *P? similis* from *P. inquirenda* by the (supposed) occurrence of *P? similis* above the Cretaceous–Tertiary boundary. Dorf (1938, 1942) made *P? similis* a synonym of *P. inquirenda*.

Berry (1932) correctly identified as a fruit the first undehiscent specimen of this fossil to be described, which he named *Sterculiocarpus coloradensis*. *Sterculiocarpus* is a form genus of fossil fruits with a superficial resemblance to certain fruits of the extant eudicot family Sterculiaceae. After dehiscent and undehiscent specimens of *Palaeoaster* were found together at several localities, Dorf (1938, 1942) suggested and Brown (1943) agreed that *S. coloradensis* is a synonym of *P. inquirenda*. Neither author made a formal synonymy.

The paleobotanical literature includes two significant errors of identification relevant to *Palaeoaster*. Marty (1907: 12–14, pl. 1, fig. 3) figured a single specimen from the Tertiary of Europe that he confidently assigned to *E? porosum*. The specimen, IRSNB 68664, does not belong to this spe-

cies. Lesquereux (1873: 400) briefly described a single specimen that he tentatively assigned to *Eucalyptus haeringiana*? Ettingshausen. *Eucalyptus haeringiana* is a fossil species from the Tertiary of Europe, based on leaves and associated fruits that resemble the extant genus *Eucalyptus* of the primarily Australian eudicot family Myrtaceae. The figure with Lesquereux's reprinted description (Lesquereux, 1878: 296, pl. 59, fig. 10) shows *Palaeoaster* specimen USNM 488. This specimen, cited by some of Lesquereux's contemporaries as *Eucalyptus haeringiana*? Lesquereux (i.e., not Ettingshausen), was excluded from *Eucalyptus* and left *incertae sedis* by Maiden (1924: 222); Knowlton (1930: 133) considered this specimen to be "probably . . . congeneric" with Lesquereux's (1874) *Eriocaulon? porosum*.

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Literature Cited

- Berry, E. W. 1932. A sterculiaceae fruit from the lower Eocene (?) of Colorado. *J. Wash. Acad. Sci.* 22: 119–121.
- Brown, R. W. 1943. Cretaceous–Tertiary boundary in the Denver Basin, Colorado. *Bull. Geol. Soc. Amer.* 54: 65–86, 2 plates.
- . 1962. Paleocene flora of the Rocky Mountains and Great Plains. *Profess. Pap. U.S. Geol. Surv.* 375.
- Chesters, K. I. M., F. R. Gnauck & N. F. Hughes. 1967. Angiospermae. Pp. 269–288 in W. B. Harland et al. (editors), *The Fossil Record*. Geological Society of London.
- Coulter, J. M. & C. J. Chamberlain. 1903. *Morphology of angiosperms*. D. Appleton, New York.
- Daghlian, C. P. 1981. A review of the fossil record of monocotyledons. *Bot. Rev.* 47: 517–555.
- Dorf, E. 1938. Upper Cretaceous floras of the Rocky Mountain Region. I. Stratigraphy and palaeontology of the Fox Hills and lower Medicine Bow formations of southern Wyoming and northwestern Colorado. *Publ. Carnegie Inst. Wash.* 508: 1–78.
- . 1942. Upper Cretaceous floras of the Rocky Mountain region. II. Flora of the Lance Formation at its type locality, Niobrara County, Wyoming. *Publ. Carnegie Inst. Wash.* 508: 79–159.
- Gale, H. S. 1910. Coalfields of northwestern Colorado and northeastern Utah. *Bull. U.S. Geol. Surv.* 415.
- Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland & D. L. Hawksworth (editors). 2000. *International Code of Botanical Nomenclature (St Louis Code)*. *Regnum Veg.* 138.
- Horwood, A. R. 1912. The past history of monocotyledons, with remarks on their origins. *Scott. Bot. Rev.* 1: 164–180, 216–234.
- Knowlton, F. H. 1917. Fossil floras of the Vermejo and Raton formations of Colorado and New Mexico. *Profess. Pap. U.S. Geol. Surv.* 101: 223–435.
- . 1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *Bull. U.S. Geol. Surv.* 696.
- . 1922. The Laramie flora of the Denver Basin, with a review of the Laramie problem. *Profess. Pap. U.S. Geol. Surv.* 130.
- . 1930. The flora of the Denver and associated formations of Colorado (posthumous, edited by E. W. Berry). *Profess. Pap. U.S. Geol. Surv.* 155.
- Lee, W. T. 1912. Coal fields of Grand Mesa and the west Elk Mountains, Colorado. *Bull. U.S. Geol. Surv.* 510.
- Lesquereux, L. 1873. Lignitic formation and fossil flora. Pp. 317–427 in F. V. Hayden (editor), *Sixth Annual Report of the United States Geological Survey of the Territories; embracing portions of Montana, Idaho, Wyoming, and Utah, being a report of progress of the explorations for the year 1872*. Government Printing Office, Washington, D.C.
- . 1874. The lignitic formation and its fossil flora. Pp. 365–425 in F. V. Hayden (editor), [Seventh] *Annual Report of the United States Geological and Geographical Survey of the Territories, Embracing Colorado, Being a Report of Progress of the Exploration for the year 1873*. Government Printing Office, Washington, D.C.
- . 1878. Contributions to the fossil flora of the Western Territories. Part 2. The Tertiary flora. Report of the United States Geological Survey of the Territories, vol. 7. Government Printing Office, Washington, D.C.
- Maiden, J. H. 1924. Fossil plants attributed to *Eucalyptus*. Pp. 168–190, 219–244 in J. H. Maiden, *A Critical Revision of the Genus Eucalyptus*, Vol. 6. Alfred James Kent, Government Printer, Sydney, New South Wales.
- Marty, P. 1907. Études sur les végétaux fossiles du Trieu de Leval (Hainaut). *Mém. Mus. Roy. Hist. Nat. Belgique* 5: 1–52, 9 plates.
- Němejc, F. 1975. *Paleobotanika*, vol. 4. Nakladatelství Československé Akademie Věd, Praha.
- Smith, U. R. 2000. *Palaeoaster* (Papaveraceae), the Cretaceous Poppy. Ph.D. Dissertation, Yale University, New Haven, Connecticut.
- . In press. Permineralized fossil fruits of *Palaeoaster*, a Late Cretaceous genus of Papaveraceae. *Int. J. Plant Sci.*